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Examensarbete i ämnet biologi
Department of Wildlife, Fish, and Environmental studies
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Abstract

The aim of this study was to test whether behaviorally mediated effects of gray wolf (*Canis lupus*) presence were visible in terms of browsing intensity by moose (*Alces alces*) on tree saplings in recently planted clear-cut areas in Sweden. The study involved two different spatial scales; the clear-cut scale and tree scale. At the clear-cut scale the influence of wolf predation risk, tree density and tree height on moose browsing intensity was evaluated. At the individual tree scale, the factor distance to the nearest forest edge was also included. Browsing intensity was measured as apical shoot browsing and lateral shoot browsing in 24 different recently planted clear-cuts. Due to differences in preference between tree species and qualitative differences between plant parts, the same analyses were conducted for the five main tree species and for apical and lateral shoot browsing separately. Based on pellet group counts, moose is most likely the main browser in this study. Further, I found that both tree density and tree height were lower in the wolf core areas, suggesting multicollinearity between wolf utilization, tree density and tree height at the clear-cut scale, the effect of these factors could not be separated in the multivariate models. At the clear-cut scale browsing intensity decreased with tree density. At the tree scale, although wolf utilization was an important factor explaining the variation in browsing intensity, the browsing probability decreased with tree height. Overall, this suggests that moose foraging and thus its browsing intensity was more influenced by tree density and tree height than predation risk by wolves. It also seemed that moose browse through a clear-cut area irrespectively of distance to the closest forest edge.

Keywords: Moose, browsing intensity, wolf, spatial scales, distance to forest edge, tree height and tree density

Introduction

Recent studies have shown that predators have both direct and indirect effects on herbivore prey species that may trickle down to lower trophic levels such as the plant level (Ripple & Beschta, 2004; Schmitz, Hambäck, & Beckerman, 2000). Predators may directly influence herbivore populations by killing individuals of the population or indirectly by changing the movement patterns towards less risky habitat types, increasing vigilance behavior or increasing group size (Kuijper et al., 2013). These direct and indirect effects have both the potential to alter herbivore browsing patterns and intensity. Browsing intensity is likely to decrease when less herbivores are present and in high risk habitat types that they avoid (Kuijper et al., 2013).

In the 1960s the gray wolf (*Canis lupus*) was extinct in all of Scandinavia. After the settlement of a few wolves from the Finnish-Russian population (Zimmermann, 2014), the population in Scandinavia rapidly increased from only a few individuals in the 1980s to 380 wolves during the winter 2012- 2013 (Vila et al., 2003; Wabakken et al., 2001; Zimmermann, 2014). Their distribution is mainly confined to the south-central parts of Sweden (Wikenros, 2009). Wolves inhabit a variety of habitats with a range of prey species available (Zimmermann, 2014). Both moose (*Alces alces*) and roe deer (*Capreolus capreolus*) are important prey species, but moose is their main prey species in Sweden (Sand et al., 2008).

This thesis focuses on the indirect effects of the gray wolf on ungulate populations in terms of browsing intensity on the clear-cut scale and tree-scale. Besides predation risk, various other variables influence ungulate browsing and foraging patterns at different spatial scales (Bergqvist et al., 2001; Danell et al., 1991; Lindqvist, 2012). This study focuses on clear-cut scale and tree-scale.

Clear-cut scale

According to Rettie and Messier (2000) habitat selection reflects the avoidance of factors negatively influencing individual fitness. For herbivore prey species one important trade-off is the one between predation risk and access to foraging sites (Massé & Côté, 2009). Dussault et al. (2005) showed that predation risk, and food availability were the most important factors influencing moose winter habitat selection and thus browsing patterns at this scale.

Swedish forests are intensively managed creating a heterogeneous landscape consisting of forest stands of different ages and clear-cut areas of different sizes (Edenius et al., 2015). Food availability is generally higher in open areas i.e. recently planted clear-cut areas, where higher light availability promotes understory plant abundance (Massé & Côté, 2009). Massé and Côté (2009) showed that white- tailed deer habitat selection in absence of predators is mainly driven by forage acquisition, resulting in that this species is therefore more often found in open areas (Massé & Côté, 2009).

At any given site predation risk is influenced by two things: 1. the probability of a prey detecting a predator (visibility) and 2. the probability for a prey to escape when attacked (Ripple & Beschta, 2004). A moose standing in an open area can be detected more easily by predators and has a greater difficulty reaching the relative protection of cover (Hamilton et al., 1980). Compared to felids which use stalking as a hunting strategy, canids (including wolves) often exhaust prey by chasing them and therefore have more successes when hunting in open areas (Wikenros et al., 2009). As a result ungulates may try to avoid the more risky open areas under predation risk, suggesting that browsing intensity was lower in these areas.

Tree-scale

Possible factors influencing browsing on individual trees within a clear-cut include: distance to the forest edge, tree density and tree height. (Andren & Angelstam, 1993; Matlack, 1993).

Thus, whereas food availability is higher in open areas whereas forests may provide protection in relation to predation risk (Hamilton et al., 1980). With the presence of predators ungulates may perceive the center of the clear-cut as more risky compared to the forest edge, resulting in differences in browsing intensity at different distances from the forest edge. Andren and Angelstam (1993) concluded that in absence of predators damages made by moose browsing in clear- cuts was not related to distances from a forest edge. Further, Hamilton et al. (1980) showed declining trends of moose browsing with greater distance from the forest edge in absence of predators and concluded that there is no ultimate limit to the distance moose forage from the forest edge into a clear- cut area.

Furthermore, both tree density and tree height may influence ungulate browsing intensity. According to Vivas and Saether (1987) the proportion of trees browsed decreased linearly with tree density. Wallgren et al., (2013) showed that pine damage due to moose browsing declined with pine stem density. They explained this through a negative effect of density on food quality. At a stem density of 8000 stems/ha and higher a strong competition between trees resulted in trees with only small shoots and little browse biomass. As a consequence, no or little moose browsing damage was observed (Wallgren et al., 2013). In terms of tree height, Markgren (1969) showed that browsing animals mostly select juvenile plants, young shoots and leaves, since they contain high levels of nitrogen. This finding is supported by (Koster, 2012) who found that moose preferred to browse on smaller trees with a tree height up to 0.5m.

Overall, qualitative factors influence ungulate browsing patterns (Palo et al., 1992). Moose are suggested to select shoots with high energy intake relative to chemical defense substances (Lindqvist, 2012). Apical shoots of higher quality may therefore be selected over lateral shoots of lower quality (Lindqvist, 2012). Moreover, moose prefer to browse on different tree species. Scots pine (*Pinus silvestris*) and Norway spruce (*Picea abies*) are the most important commercial tree species in Sweden consisting of 80,2% of the standing volume of productive forests (Loman, 2010). Although moose do not prefer Scots pine, it is the dominant species in moose winter diet (Andren & Angelstam, 1993; Bergqvist et al., 2001). In general, moose prefer to browse on deciduous tree species (Andren & Angelstam, 1993; Courtois et al., 2002). Ahlén (1975; as cited in Andren & Angelstam, 1993) showed that moose prefer to browse on Rowan (*Sorbus aucuparia*) > Birch (*Betula pubescens* and *Betula pendula*) > Pine (*Pinus sylvestris*). Under predation risk moose may take more risk for the most preferred tree species or qualitatively higher plant parts as potential gains increase.

In summary ungulate browsing patterns are influenced by many different factors across different spatial scales. Especially little is known about browsing patterns in young forest stands under wolf predation risk. Understanding the effect of ungulate diet selection in presence of large predators may be an important aspect for Sweden forestry and it is therefore critical for managing both wildlife populations and forestry practices. The aim of this study was to test whether any indirect effects of wolf presence could be detected in browsing intensity on tree saplings in recently planted clear-cut areas in Sweden. Different core hypotheses were formulated and tested:

At the clear-cut scale, I tested whether browsing intensity differed in areas with and without predation risk. Due to the trade-off between forage acquisition and predation risk, I expected that the proportion of apical and lateral shoots browsed should be higher in areas outside wolf home ranges compared to areas inside the wolf core areas.

At the tree- scale, different hypotheses were tested:

I. I tested whether browsing patterns inside recently planted clear-cuts changed in relation to distance from the forest edge under risk of wolf predation. I expected that in wolf core areas the proportion browsed is higher in closer proximity to the forest edge which may provide protection. Further I expected that browsing would show a stronger decrease more strongly with an increasing distance from the forest edge in wolf core areas as compared to areas outside wolf home ranges where ungulates feel safe and thus continue to browse randomly in greater distances from the forest edge.
II. Second, I tested whether qualitative food distribution influenced browsing intensity differently under predation risk. I expected that the browsing intensity on the qualitatively higher apical shoots is higher in wolf core areas compared to areas outside wolf home ranges.
III. Last, I expected that browsing intensity on preferred tree species would be higher in wolf core areas compared to areas outside wolf home ranges.

Methods

Study Area

The study area was located in the Swedish boreal forest zone in the counties of Västmanland, Dalarna, Närke and Värmland. The area is intensively managed with different forest activities such as primarily cleaning, thinning and final felling. This forestry management results in a mosaic landscape characterized with clear-cuts of different sizes and forest stands of different ages. The forests are mainly composed of Norway spruce (*Picea abies*) and Scots Pine (*Pinus sylvestris*) (Andren & Angelstam, 1993). Deciduous tree species such as Silver birch (*Betula pendula),* Downy birch *(Betula pubescens*) and Rowan (*Sorbus aucuparia*) are abundant in clear-cuts (Andren & Angelstam, 1993; NordGIS). Wolves inhabit a major part of South-Central Sweden. In the winter of 2009/2010 the entire wolf population was estimated at 252-291 wolves, consisting of 28 packs and 21-24 pairs (Wikenros, 2011). In 2012-2013 the entire wolf population in Scandinavia was estimated at 380 wolves, of which Sweden was home to the majority (Zimmermann, 2014). In this study the potential influence of three different packs of wolves on the browsing patterns and intensity of moose were evaluated, since moose (*Alces alces*) is their main prey species in Sweden. Other browsers present but at a much lower density an browsing impact on plants in the study area are red deer (*Cervus elaphus*) and roe deer (*Capreolus capreaolus*). Around the Grimsö Wildlife Research Area, located in the center of the study area, moose winter densities were estimated at 12.5 ± 1.54 per 1000ha using pellet group counts (Lindqvist, 2012). Roe deer occur at lower densities compared to moose (Edenius et al., 2015; Personal communication H. Sand) with an estimated population density of 9.87 ± 1.48 per 1000ha in 2011 (Lindqvist, 2012). Moose diet mainly consists of Scots pine and several deciduous trees (Andren & Angelstam, 1993). In contrast, herbs, shrubs and grasses are more dominant in deer diet (Gill, 1992). When roe deer do browse on trees, needles and buds form a big part of the diet (Bergquist & Örlander, 1996). Exact ungulate densities for the whole study area were unknown. Based on above described browsing differences and higher moose densities in a part of the study area, I assumed that most browsing in this study area is caused by moose.

Experimental design

To create the contrast in high versus low intensity of wolf utilization I used annual wolf pack home ranges based on intense wolf monitoring by the Scandinavian Wolf Research Project (Skandulv) between 1999 and 2015 (www.slu.se/skandulv). Wolf monitoring is based on a combination of three methods, namely snow tracking, scat DNA- analysis and radio telemetry (Liberg et al., 2011). These techniques can be combined to estimate the number of animals in a pack, verifying reproductions and to distinguish between different wolf packs (Liberg et al., 2011). Using ArcGIS 10.2.2, I first mapped the home ranges of three different packs at the time of study (2014-2015). For these three pack home ranges I then used information of spatial location of the annual home ranges for each year during 1999-2015 and calculated the area within each present home range where annual wolf home ranges overlapped for at least 9 – 15 years out the last 17 years. A maximum overlap of 15 was chosen, since none of the areas overlapped more than 15 years. This area within the present home range was defined as the pack's core area (red areas in fig. 1). Since I used 3 packs, I ended up with 3 core areas (fig. 1). I linked each of these core areas with an area that was not included in any of the annual wolf home ranges between 1999 and 2015. These areas outside wolf home ranges are most likely only visited by single dispersing wolves, since the annual monitoring of the wolf population is limited to wolf pairs and packs. Based on Carbyn and Trottier

(1987) I assumed that single wolves pose a limited threat to moose and therefore do not have a potential for exerting similar large indirect effects on moose browsing pattern as did packs and pairess . As a result, I termed these areas outside wolf home ranges, the low wolf utilization areas. The outer edge of low wolf utilization areas were located at least 3km from all annual 1999-2015 wolf home ranges to account for the fact that the size of the home ranges recorded may have been slightly underestimated the actual pack home range size (personal communication, Håkan Sand). This experimental design resulted in 3 pairs of a wolf core area (high wolf utilization) and outside wolf home ranges (low wolf utilization). In each of these six different areas I selected four different clear-cuts (24 in total) for estimation of browsing intensity.

Clear-cuts were selected based on a database provided by the Swedish Forest agency (Skogsstyrelsen), including the spatial location and age of clear-felled areas. Selected clear-cuts were felled between 2008 and 2010 and planted between 2009 and 2011. This resulted in an average tree height of 83cm for all clear-cuts. I selected clear-cuts of this average height based on moose and wolf height assuming that moose can easily spot wolves and vice versa at this height as it is too low to function as a protective cover for moose. Moose home range sizes range from 13.7km2 for females to 25.9km2 for males (Cederlund & Sand, 1994). To make sure the different clear-cuts are visited by different moose and therefore independent from each other, all selected clear-cuts were at least three kilometers apart.

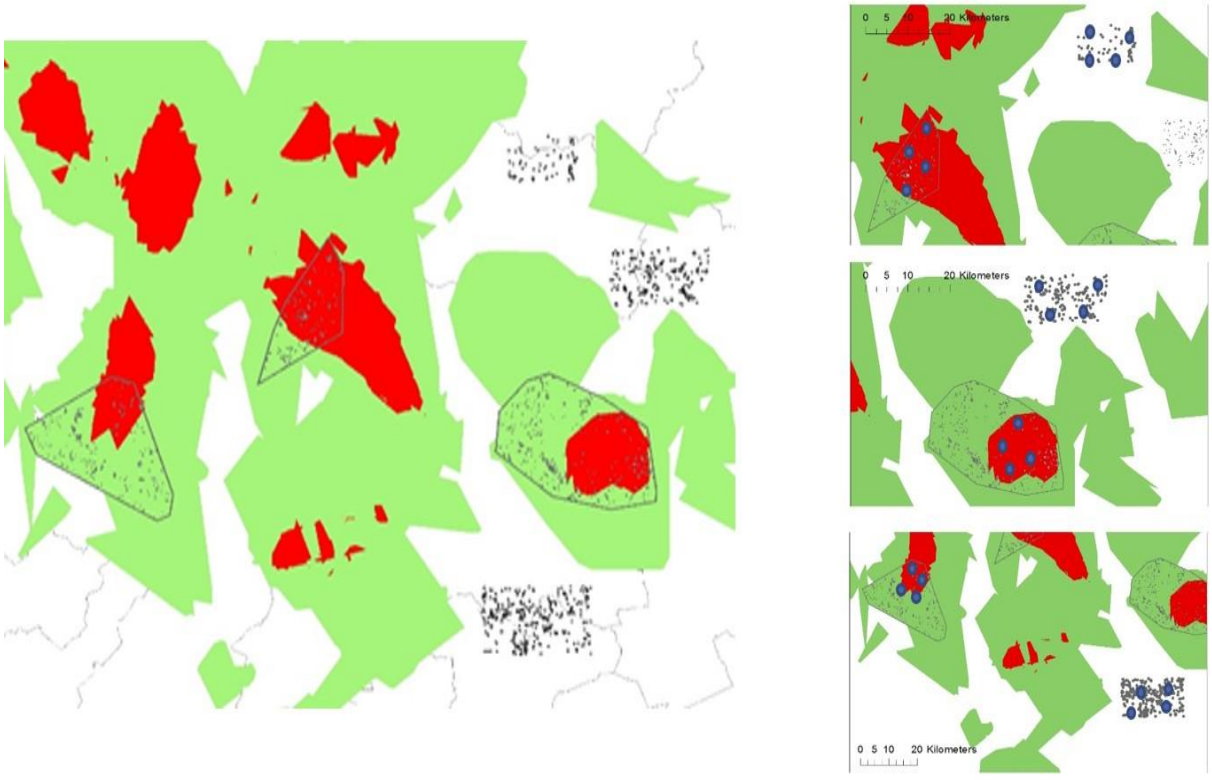

Figure 1: Left: Shows entire study area. Green: all wolf home ranges 1999-2015. Red: Wolf core areas where wolf home ranges overlap for 9-15 years. The big polygons represent the current home ranges of the three different wolf packs. And the black dots are the clear-cuts inside wolf core areas and outside wolf home ranges. Right: Wolf core area (red) paired with area outside wolf home ranges for each wolf pack. The blue dots represent the measured clear-cuts and the blacks dots represent all clear-cuts.

Measurements of browsing intensity

Browsing intensity was measured in all 24 clear-cuts in October 2015. In each clear-cut browsing was measured along two line transects which were perpendicular to each other. One transect line was set in northern and one in eastern direction to the forest edge. I used these two cardinal directions to reduce confounding effects of variation in sun shading effects of the forest edge, which can influence browsing intensity between different clear-cuts (Matlack, 1993). In some clear-cuts measurements in northern and/or eastern cardinal directions were not possible (e.g. due to dirt roads or lack of a clear forest edge) and in those cases transect lines were set in a direction as close possible to the northern or eastern direction. Transect lengths varied between 39- 138m, depending on the shape of the clear-cut. Starting from the forest edge, each tree within a maximum distance of 0.5m on each side of the transect line was measured. Only trees between 40 to 350cm were recorded, as they fall within moose browsing range (Kalén & Bergquist, 2004). Moose browsing can be divided in 1) browsing of apical shoots and 2) browsing of lateral shoots (Bergqvist et al., 2001). Similar to Kuijper et al. (2013), I measured apical shoot browsing and browsing of the top 10 lateral shoots. Apical shoots have the highest chance to be browsed and such browsing is the main factor slowing down tree growth (D. Kuijper et al., 2013). Stem breakage was not included since it is ambiguous whether the damage is caused by browsing or something else. Bark stripping was also not measured, since the average tree height is 83cm and therefore too low to result in extensive bark stripping. For each tree within 0.5m of the transect length browsing was recorded the following two ways: 1. Apical shoot browsing yes or no and 2. The total number of the top 10 lateral shoots browsed. I used a slightly different approach for deciduous than for the coniferous species in terms of lateral shoot browsing. Conifers form the bulk of moose winter diet, however deciduous are more preferred during summer (Andren & Angelstam, 1993; Courtois et al., 2002). Since I conducted the study in October, it was too early to see browsing during the current fall on Scots Pine. To account for this difference in time of browsing I measured browsing on conifers the following way; first, I measured whether the current apical shoot was browsed yes or no. Second, I looked at the apical shoot of previous year and checked if it was browsed before. If this was the case, a lateral shoot had taken over the apical dominance or a thickening at the base of the new apical shoot could be seen. If the apical shoot was browsed the previous year, it was counted as one of the top10 lateral shoot browsing.

Besides browsing, the distance to the closest forest edge was measured for each tree individual using a Nikon Forestry Pro laser for each individual. Because, tree height and tree density may influence browsing intensity tree height was measured for each individual and tree density was calculated at clear-cut scale after data collection. Because my main hypotheses were focused on predation risk the clear-cuts measured were not pre-selected based on tree density or differences in tree height below 1m. Finally, any signs of human activity such as feeding stations, high hunting seats and dirt roads were noted.

Pellet count

To receive a relative estimate of ungulate density and to find out which species is mostly present in the study area and to test the effects of wolf utilization on ungulate densities, pellet group counts were made. In all 24 clear-cuts the same transect line was walked again and the number of pellet groups for each ungulate species within a maximum distance of 1m on each side of the transect line was counted. To determine the effects of open areas versus forests (stands) on ungulate densities I repeated the estimate along a transect line of the same length into the forest.

Statistical analysis

Pellet count

First, the percentage of pellet groups found for each ungulate species was calculated for the entire study area. Relative ungulate densities were calculated as the total number of pellet groups found divided by the total transect length (m) of each stand. This number was divided by two, since measurements were done within a maximum distance of 1m on each side of the transect length. To test for the effect of wolf utilization on ungulate densities, the ungulate densities in the open area and forest were averaged for each clear-cut. A Mann Whitney- U test was used to evaluate the difference in visitation inside wolf core areas versus outside wolf home ranges. Each clear-cut was spatially different and the data was therefore not paired. Differences in ungulate densities between forests and open areas were evaluated using a Wilcoxon signed-rank test. In each recently planted clear-cut measurements continued along a transect line through two different stands (Open area and Forest). As a result these measurements were not independent and a paired test was used. Last I combined the different wolf utilization treatments and the stand treatments, resulting in four different groups (Open/High, Open/Low, Forest/High and Forest/Low). Differences among these groups were tested using a Kruskal- Wallis test.

Browsing intensity

For every tree measured along the transect line apical shoot browsing was recorded as “browsed” (1) or “not browsed” (0). The proportion lateral shoot browsing was calculated as the number of top 10 lateral shoots browsed divided by the total amount of lateral shoots present with a maximum of 10. I also combined apical and lateral shoot browsing into a new binomial variable “total browsing”. When apical shoot browsing was 1 or the proportion of lateral shoots > 0.0, total browsing was recorded as “browsed” (1). When the apical shoot was not browsed and none of the top10 lateral shoots was browsed, total browsing was recorded as “not browsed” (0). This was repeated for each individual tree measured. Concluding, I ended up with three response variables; apical shoot browsing (yes/no), total browsing (yes/no), and proportion of top10 lateral shoots browsed.

Clear-cut scale

At the clear-cut scale I tested which variables had an effect on the browsing intensity between different recently planted clear-cuts. Average tree height was calculated for each clear-cut and browsing intensity was described as a proportion. As discussed before, different plant parts may have a different influence on ungulate browsing. As a result a distinction was made between total, apical shoot and lateral shoot browsing. The proportions of total and apical shoot browsing were calculated as the number of trees within one clear-cut with total or apical shoot browsing divided by the total number of trees measured in the clear-cut. The proportion of lateral shoot browsing within a clear-cut was calculated as the number of trees with a proportion of lateral shoot browsing > 0.0 divided by the total number of trees measured in the clear-cut.

Before analyses all three response variables were arcsine transformed to normalize proportional data. To test the effect of different factors on browsing intensity between the 24 different clear-cuts a linear mixed-effect model was used. Different models were analyzed with either the proportion of total browsing, apical shoot browsing or lateral shoot browsing as the response variable. Wolf utilization level (high or low) nested in wolf pack was the random effect. Moreover I added a spatial correlation structure which accounted for the variance in distance among the different clear-cuts. As

discussed in the introduction the core hypothesis at this scale was related to wolf utilization, however tree density and tree height may also influence browsing intensity. These three variables were therefore chosen as fixed factors. Due to the high correlation among these three variables (see results), three univariate models were created and their model fit was tested using the corrected AIC (AICc) instead of the AIC (Akaike information criterion) due to the small number of observations. Based on the AICc between the different univariate models I chose the model with the lowest AICc value. According to Burnham and Anderson (2002) an AIC difference of 0-2 gives substantial empirical support of two models to be similar. Therefore I showed the results of all models with $\Delta AICc \leq 2$.

The above procedure was followed for all tree species together and subsequently for the five most abundant tree species separately.

Tree-scale

Here I explored which variables influenced browsing intensity of an individual tree within clear-cuts. On this scale the core hypotheses were related to wolf utilization and distance to the closest forest edge. Following from the above, individual tree height and tree density may influence browsing intensity as well. At this scale, I used the binomial response (yes or no browsing) for total tree browsing and apical shoot browsing measured for each individual tree within the clear-cut. I used a generalized linear mixed model with a binomial family to analyze which of the four factors above influenced the probability of a tree being browsed. As random factor wolf utilization (high or low) and clear-cuts were nested in wolf pack. The proportion of top10 lateral shoots browsed was already calculated for each individual tree, as described above. To analyze the effects on the proportion lateral shoots browsed a linear mixed effect model was used. Wolf utilization (high or low) and clear-cuts nested in pack was the random effect.

To test which of the four factors had an effect on browsing intensity I created four univariate models using these variables, and multivariate models with the different combinations of these variables (with 2 fixed effects, respectively). Three way interactions were avoided, since it is challenging to interpret its results correctly. Model selection was based on the AIC and ΔAIC. First, the four univariate models were tested separately. Based on the core hypotheses wolf utilization and distance were preferably included in the multivariate models. When the univariate model with either tree density or tree height had a better model fit compared to the univariate models with wolf utilization or distance, these former variables were included in the multivariate models with wolf utilization and distance. As a result, four different univariate and several multivariate models were created and their AIC's compared. For each browsing response the model with the lowest AIC or the models with a $\Delta AIC \leq 2$ were selected.

Again, the above procedure was followed for all tree species together and subsequently for the five most abundant tree species separately.

Results

Pellet count

In total 46 different pellet groups were found during the whole study. Moose represented 78.2% and roe deer represented 8.7% of the total. The other 13% could not be identified, mostly due to weather conditions, and were defined as “unknown”. The number of pellet groups found within the open areas did not differ from the number found in the forest (P = .70). Wolf utilization seemed to have an effect on the number of pellet groups found in the study area, although this was only a trend (p < 0.1). Fewer moose pellet groups were found in the high wolf utilization areas (P = .08). Last, there is no difference between the four different groups resulting from the combination of the wolf utilization and the stand treatment (P=.348).

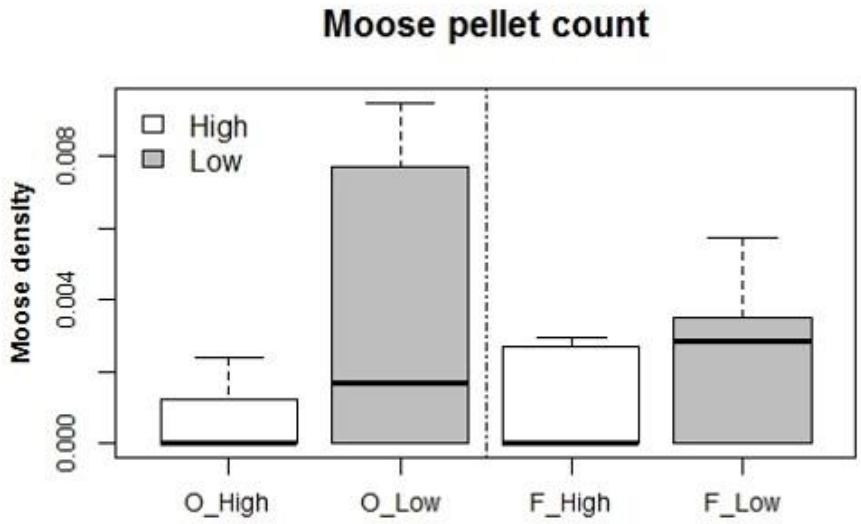

Figure 2: Moose densities between wolf utilization and stand treatments.

General characteristics of study plots

In total 3173 tree saplings were measured in the 24 different clear-cuts. *Betula pubescens* and *Betula pendula* were the most dominant tree species, followed by *Picea abies*, *Sorbus aucuparia* and *Pinus sylvestris*. These five species represented 98.7% of all tree saplings measured. Other tree species accounted for 1.3% of all measured trees and were therefore not used for individual species analyses. Table 1 shows the general characteristics of the sampled area inside wolf core areas and outside the wolf home ranges.

Table 1: Characteristics sampled area.

Description	Inside wolf core area	Outside wolf area
Total number of clear-cuts	12	12
Total number of trees	1148	2025
Total browsing (%)	34.0	25.7
Apical shoot browsing (%)	13.3	10.4
Lateral shoot browsing (%)	32.2	23.9
Mean tree density clear-cut (m^{-2})	0.78	1.36
Mean tree height clear-cut (cm)	72.0	88.4
Nr of Betula pendula	647	253
Nr of Betula pubescens	737	516
Nr of Picea abies	344	239
Nr of Pinus sylvestris	125	107
Nr of Sorbus aucuparia	133	32

Clear-cut scale

Treatment characteristics

The core hypothesis was related to wolf utilization. In addition tree density and tree height may influence browsing intensity. I assumed that due to the number of replications and randomization of sampling (i.e. not pre-selecting clear-cuts based on tree density and tree height), both factors would not differ between different wolf utilization levels. However, due to their potential influence on browsing intensity I first tested this assumption using the student t-test.

Unfortunately, tree density was higher in the low wolf utilization areas (P=.002) and the average tree height was also higher in the low wolf utilization areas (P=.002) (Figure 3).

These results suggest multicollinearity between wolf utilization and the two different variables tree density and average tree height. As a result wolf utilization could not be analyzed in the same model with tree density or average tree height. Instead these three variables were tested separately as univariate models. As described above, the AICc and ΔAICc were used to select the model explaining most of the variation in browsing intensity.

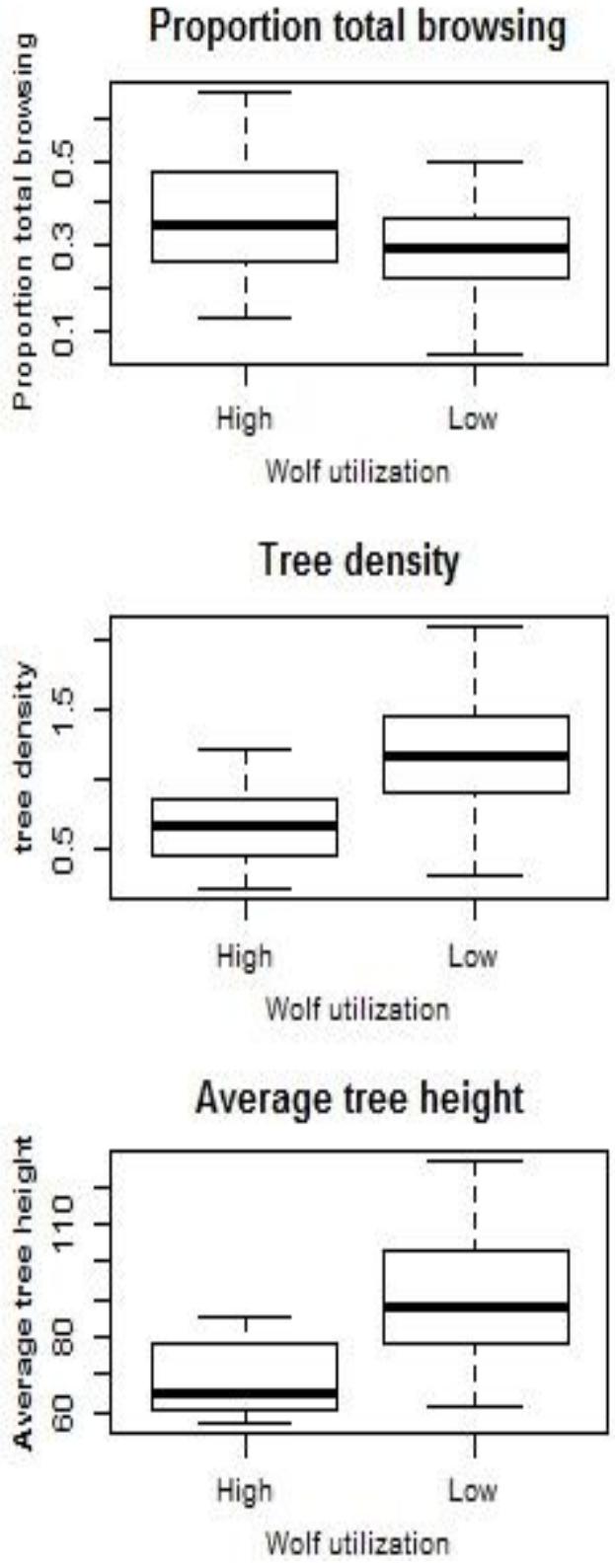

Figure 3: Characteristics of proportion total browsing, tree density and average tree height between the different wolf utilization levels.

Clear-cut scale browsing

Based on the AICc and the ΔAICc I conclude that the amount of variation explained by tree density was highest for all three browsing variables (Table 2). Their results are summarized in table 3.

Table 2: Model selection factors influencing browsing intensity for all species combined between clear-cuts. The bold models are the models which are tested based on their AICc and ΔAICc.

Browsing variable	Fixed factor	AICc	ΔAICc
Total	**Tree density**	**-3.44**	***0***
	Wolf utilization	-0.49	2.95
	Average tree height	3.31	6.75
Apical shoot	**Tree density**	**-37.50**	***0***
	Wolf utilization	**-36.04**	**1.46**
	Average tree height	-34.65	2.85
Lateral shoot	**Tree density**	**-5.14**	***0***
	Wolf utilization	- 2.22	2.92
	Average tree height	2.06	7.20

From these tables I can conclude that tree density influenced the proportions total and lateral shoot browsing between clear-cuts. Where the proportion browsed decreased with tree density. For the proportion apical shoots browsed there seemed to be a trend towards a decline in browsing intensity with tree density. Wolf utilization was kept in the model for the proportion apical shoots browsed although it did not influence its proportion browsed.

Table 3: Results of selected models of browsing at clear-cut scale for all tree species together. Significant effects ($P < 0.05$) are indicated in bold

Browsing variable	Fixed factor	Value	P-value
Total	**Tree density**	**-0.130**	**0.047**
Apical shoot	Wolf utilization	-0.035	0.352
	Tree density	-0.052	0.086
Lateral shoot	**Tree density**	**-0.135**	**0.031**

The proportion of all three browsing variables, differed between tree species (kruskal-wallis, all P<.001). The total percentage browsed of each species was calculated as the number browsed trees divided by the total number of trees, times 100. Their results are summarized in table 4, and are ranked from most to least preferred based on the total browsing.

Table 4: Differences in browsing intensity between species.

Species	Total	Apical shoot	Lateral shoot
Sorbus aucuparia	94.5	64.2	92.1
Pinus sylvestris	30.7	3.0	30.7
Betula pubescens	29.7	12.4	27.5
Betula pendula	27.0	64.2	24.4
Picea abies	8.2	0.9	7.9

As a result, the above explained models were analyzed for each tree species separately. Based on the model selection, the importance of both tree density and wolf utilization were highlighted for all species. The tables for model selection for each tree species and their results can be found in Annex 1. *Betula pubescens* and *Betula pendula* were the most common tree species in the study area. For *Betula pubescens* the proportion total browsing (P=.028) and the proportion lateral shoot browsing (P=.032) both decreased with tree density. Wolf utilization had the best model fit for apical shoot browsing, however it did not influence its proportion browsed. For *Betula pendula* multivariate models with wolf utilization and tree density had the best model fit. Average tree height was also included in the lateral shoot browsing. Its proportion lateral shoots browsed decreased with tree density (P=.031) and slightly decreased with tree height (P<.001). Further, there was a trend towards decreased browsing with tree density for both its total proportion browsed (P.052) and apical shoot browsed (P=.075). Wolf utilization had no effect on all three browsing responses. For the other tree species (*Picea abies*, *Pinus sylvestris*, *Sorbus aucuparia*) both wolf utilization and tree density were the most important factors explaining the variation. However, none of these factors had an effect on the three browsing responses of these tree species.

Tree scale

At this scale the response was the individual tree within the clear-cuts. Again, the core hypothesis was related to wolf utilization and distance to the nearest forest edge and these were therefore preferably included in the multivariate models. However in some cases the univariate models with either tree height or tree density had a better fit compared to the univariate models with wolf utilization or distance. Different univariate and multivariate models were analyzed for all species combined. Table 5 shows the AIC values and model selection for the proportion of total browsing.

Table 5: Model selection proportion total browsing within clear-cuts. The bold models are the models which are tested based on their AIC and ΔAIC.

Fixed factor	AIC	ΔAIC
Tree height	**3621,5**	**0**
Wolf utilization + Tree height	**3622,8**	**1.3**
Wolf utilization + Distance + Tree height	3624,5	3.0
Wolf utilization	3636,5	15.0
Distance	3636,6	15,1
Tree density	3637,7	16,2
Wolf utilization + Distance	3638,3	16,8
Wolf utilization * Distance	3638,7	17,2

The univariate model with tree height explained most of the variation and was therefore included in the multivariate models with wolf utilization and distance. The multivariate model with both wolf utilization and tree height explained a similar amount of variation as the univariate model with tree height. Therefore, results of both models were shown. Model selection was similarity conducted for apical shoot browsing and lateral shoot browsing (table in Annex 2). The results for all three browsing variables for all tree species together are summarized in table 6.

Table 6: Results of selected models of browsing at tree-scale for all tree species together. Significant effects (P < 0.05) are indicated in bold.

Browsing data	Fixed factor	Value	P-value
Total	Tree height	-0.005	0.000
	Wolf utilization +	-0.223	0.408
	Tree height	**-0.005**	**0.000**
Apical shoot	Tree height	-0.011	0.000
	Wolf utilization +	-0.153	0.572
	Tree height	**-0.011**	**0.000**
Lateral shoot	**Tree height**	**-0.001**	**0.000**

The probability of total and apical shoot browsing declined with tree height. Wolf utilization was kept in the model, although it did not influence their browsing intensity. Last, the proportion of top10 lateral shoots browsed slightly declined with tree height. Both distance to the nearest forest edge and tree density explained too little of the variation to be kept in any of the models.

Similar tests were conducted for the different tree species separately. According to the AIC and ΔAIC wolf utilization, distance and tree height were important factors explaining the variation in both total and apical browsing for all species. In contrast with the analyzes with all tree species together, the influence of wolf utilization was highlighted in explaining the variation in browsing intensity for all species separately, since it was included in all models. Although it was included in

the lateral shoot browsing models for every species, it did not influence lateral shoot browsing for any species.

All factors that were kept in the selected models for the different species are summarized in table 7. These are only a part of the results, all results are summarized in annex 2. The probability of total browsing on *Betula pubescens* slightly declined with tree height. Further, there seemed to be a trend towards an increase in the probability browed further away from the forest edge. The probability of apical shoots browsed was higher in low wolf utilization areas and declined with tree height. Different factors influenced the browsing intensity of *Betula pendula*. Its probability of total browsing declined with increased distance to the closest forest edge. Second, at higher tree heights the probability of apical shoots browsing was lower. Again, wolf utilization was included in the models, but did not show an effect on the browsing intensity. Furthermore, the probability of total *Picea abies* browsing was higher in low wolf utilization areas and there seemed to be a trend towards a decline in the probability total browsing with distance. For *Pinus sylvestris* there seemed to be a trend towards a higher probability total browsing in low wolf utilization areas and its probability total browsing increased with tree height. Last, the probability of apical shoots browsed of *Sorbus aucuparia* seemed to increase with distance. Wolf utilization had no effect on its probability apical shoots browsed.

Table 7: Results browsing intensity for the different species within a clear-cut. Only the factors that influenced their browsing intensity are summarized here. Significant effects ($P < 0.05$) are indicated in bold.

Species	Browsing variable	Fixed factor	Estimate	P-value
Betula pubescens	Total	Wolf utilization +	-0.399	0.313
		Distance +	0.006	0.098
		Tree height	**-0.005**	**0.034**
	Apical	**Wolf utilization+**	**-0.577**	**0.044**
		Tree height	**-0.011**	**0.002**
Betula pendula	Total	Wolf utilization +	-0.539	0.128
		Distance +	**-0.008**	**0.041**
		Tree height	-0.004	0.129
	Apical	Wolf utilization +	-0.153	0.572
		Tree height	**-0.011**	**0.000**
Picea abies	Total	**Wolf utilization**	**-1.09**	**0.037**
		+ Distance	-0.011	0.096
Pinus sylvestris	Total	Wolf utilization +	-0.667	0.087
		Distance +	0.011	0.134
		Tree height	**0.016**	**0.019**
Sorbus aucuparia	Apical	Wolf utilization +	-0.081	0.888
		Distance	0.015	0.092

Discussion

The aim of this study was to test whether indirect effects of gray wolf predation risk were visible in browsing intensity on tree saplings in recently planted clear-cut areas in Sweden. Multiple variables were tested at different spatial scales. At the clear-cut scale, the proportions total and apical shoots browsed decreased with tree density when all tree species were analyzed together. Both tree density and wolf utilization were important factors explaining the variation in browsing intensity for each species separately. Although, wolf utilization did not have an effect on the browsing intensity of any of the species, the proportions browsed did seem to decrease with tree density for the two most common tree species (*Betula pubescens* and *Betula pendula*). At the tree-scale, the browsing intensity for all species together declined with tree height. Although wolf utilization was an important factor explaining the variation in the probability total shoots browsed and apical shoots browsed, it did not influence the browsing intensity. When different tree species were analyzed separately wolf utilization was highlighted in explaining the variation in browsing intensity, since it was included in all selected models for all tree species. The proportions browsed were only higher in the low wolf utilization areas for the apical shoots of *Betula pubescens* and the proportion total browsing for *Picea abies*. However as discussed above, browsing intensity declined with tree height for a few species.

Ungulate densities were unknown for the whole study area. Based on literature I assumed that browsing in the study area was mainly caused by moose. For the whole study 36 out of 40 pellet groups that were identified originated from moose. This supports the assumption that moose was the primary browser in this study. There was a trend towards more moose pellet groups in low wolf utilization areas compared to the number found in high wolf utilization areas ($P = 0.08$). This difference might be explained by wolf utilization, however tree density and height were also higher in the low wolf utilization areas (fig.3). Koster (2012); Markgren (1969) found that moose prefer to browse on younger and smaller trees. This suggests that when predation risk had no influence, moose would have preferred to visit the high utilization areas in my study where the average tree height was lower. Since more moose pellet groups were found in the areas with a higher average tree height, predation risk may influence moose visitation. According to Vivas and Saether (1987) moose did not visit plots with higher tree density any more frequently than the low-density plots, however their time spent in a plot increased with increasing tree density. As a result I cannot conclude whether the higher moose densities are a result from a higher tree density, predation risk or a combination.

Instead of wolf utilization, tree density was the best explanatory variable explaining differences in browsing intensity at clear-cut scale. As tree density increased the proportion trees browsed declined although the total number of browsed trees increased. This influence of tree density on moose browsing was shown in several studies (Vivas & Saether, 1987; Wallgren et al., 2013). It is well known that foraging is aimed at the maximization of energy intake by increasing food intake or reducing the costs of foraging. According to Vivas and Saether (1987) a higher tree density reduces the costs of foraging as search time is reduced. They also found that food availability and thus, the number of trees browsed increased with tree density (Vivas & Saether, 1987). Moreover, at high tree densities, a stronger competition leads to smaller shoots and therefore less browse biomass (Wallgren et al., 2013), resulting in a smaller proportion being browsed. Ultimately, assuming that neighboring stands or trees have low food availability or similar tree densities, at very high tree

densities there is little else to feed on, so the proportion browsed slightly increases again (Wallgren et al., 2013). Last, Vivas and Saether (1987) also found that the time spent in a patch is higher at higher densities. This seems in contrast with the result that the proportion browsed decreased with tree density (Vivas & Saether, 1987; Wallgren et al., 2013). Vivas and Saether (1987) suggest that instead of eating a bigger proportion of low quality food, moose are more likely to select the most nutritious plant parts. They found that the proportion of the more nutritious top twigs browsed was higher at higher tree densities (Vivas & Saether, 1987). This supports the results found in this study, where the proportion apical shoots browsed was higher at higher densities compared to the proportion lateral shoots browsed. At low tree densities moose are likely to consume twigs with greater bite diameter and are forced to consume more of a single tree to meet their energy requirements and reduce foraging costs (Vivas & Saether, 1987; Wallgren et al., 2013). In this study the proportion lateral shoots browsed was higher at lower tree densities and decreased rapidly with tree density. This supports the theory of Wallgren et al. (2013) that at lower tree densities there is less competition and as a result lateral shoots are longer, suggesting that more biomass is consumed by moose from a single tree. Unfortunately no data is available in this study about bite diameters to test this prediction.

Due to the strong correlation between wolf utilization and tree density, it is difficult to conclude that the difference in the number browsed is a result of tree density alone, where higher food availability results in a higher number browsed, or that wolf presence also plays a role. A possible explanation for this correlation between wolf utilization and tree density is human activity. Several studies found that human activity, particularly human settlements, was negatively related to wolf pack presence (Mladenoff et al., 1999; Oakleaf et al., 2006). I expect that in the Swedish landscape human settlements are often in the lower lying, more productive parts of the landscape. Thus, if wolves avoid these areas of higher human activity, their core areas may be limited to less productive parts of the landscape. Due to relaxed nutrient limitation in more productive areas, a higher productivity results in a higher tree density and aboveground biomass (Paoli et al., 2008). Thus, as an indirect effect of this difference in productivity between wolf core areas (low productivity) and areas outside wolf home ranges (high productivity), tree densities and tree heights may be higher in clear-cuts of similar age in the high productive areas outside wolf core areas. In conclusion, the influence of wolf predation risk cannot be ruled out. However based on the AICc values, browsing intensity was more influenced by tree density than wolf predation risk.

At tree-scale, tree height was the most important factor affecting the probability of browsing of an individual tree by moose when all species were analyzed together. Even though wolf utilization was included in the models for total and apical shoot browsing, it did not influence their browsing intensity. When all species were analyzed separately, wolf utilization was the most important factor explaining the variation in browsing intensity for each species, since it was included in all selected models. However it did only influence the probability apical shoot browsed of *Betula pubescens* and the probability total browsing of *Picea abies*. This may suggest that moose in this study are not subjected to heavy predation by wolf and as a result wolves did not have indirect effects on the browsing intensity of moose. This was supported by Andren and Angelstam (1993). Distance to the closest forest edge was included in the models of some tree species (*Pinus sylvestris* and *Sorbus aucuparia*), however it did not influence their browsing intensity. The probability total shoot browsing slightly decreased with distance for *Betula pendula*, and there was a slight positive trend for total *Betula pubescens* browsing. Since browsing intensity slightly decreased with distance for

only one species, I believe its effect is too small to conclude that distance influences moose browsing intensity. Again, this was supported by Andren and Angelstam (1993). In contrast browsing intensity decreased with tree height for a few species. This is supported by Koster (2012); Markgren (1969) who found, as discussed before, that moose prefer to browse on smaller trees with higher quality. Since wolf utilization did not influence moose browsing I assume that moose browsing within clear-cuts is primarily focused on higher quality food acquisition. The probability of apical shoots browsed decreased with tree height, suggesting that moose prefer to browse on the top shoots at lower tree heights. In contrast, the proportion lateral shoots browsed hardly decreased with tree height.

In this study *Sorbus aucuparia* was a highly preferred tree species. *Pinus sylvestris* was less present in the study area compared to *Betula pendula, Betula pubescens* and *Picea abies*. However its percentage total and lateral browsing was higher compared to both *Betula pendula* and *Betula pubescens*. This suggest that when the number of *Pinus sylvestris* would be higher, the total number of *Pinus sylvestris* browsed was most likely higher than both *Betula pendula* and *Betula pubescens*. The fact that moose prefer to browse on *Pinus sylvestris* is supported by several studies (Bergström & Hjeljord, 1987; Cederlung et al., 1980; As cited in Bergqvist et al., 2001). The percentage of apical shoot browsing in *Pinus sylvestris* is small. This is in contrast with Bergqvist et al. (2001), who found that browsing of the apical leader in *Pinus sylvestris* accounted for 75% of all damage recorded. The small percentage browsed in this study may be explained by the timing of the field work. Since the study took place in October and *Pinus sylvestris* is the main food source for moose in winter, it was too early to see recent apical shoot browsing. In this study *Sorbus aucuparia* was highly browsed and *Picea abies* was hardly browsed. As a result it was difficult to conclude why different factors caused slight differences in browsing intensity within these two species. For the two most common tree species, *Betula pubescens* and *Betula pendula,* tree density had an influence on their browsing intensity at clear-cut scale. At the tree scale, tree height explained most of the variation in browsing intensity for the different tree species. Wolf utilization or distance to the forest edge influenced browsing intensity for some species, however since these factors differed between each tree species it was difficult to conclude its effect.

In conclusion, tree density and tree height seemed to be important factors influencing moose browsing Although wolf utilization seemed to be an important factor explaining the variation, it was not the factor explaining most of the variation. When wolf utilization was included, it did not influence moose browsing patterns at the different scales. These results may suggest that predation risk by wolves was too low to have an indirect effect on moose browsing patterns in Sweden. Last, only total *Betula pendula* browsing slightly decreased with distance to the closest forest edge. This suggest that moose browse through a clear-cut area irrespectively of distance to the closest forest edge. Importantly the high correlation between wolf utilization and tree density should be evaluated, to be able to draw more conclusions their effects on moose browsing patterns across clear-cuts.

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Annex 1

Species	Browsing data	Fixed factor	AICc	ΔAICc
Betula pendula	Total	**Tree density**	**35.4**	**0**
		Wolf utilization	**35.5**	**0.1**
		Average tree height	37.9	2.4
	Apical shoot	**Wolf utilization**	**4.1**	**0**
		Tree density	**4.39**	**0.29**
		Average tree height	8.8	4.7
	Lateral shoot	**Tree density**	**33.95**	**0**
		Average tree height	**34.5**	**0.55**
		Wolf utilization	**34.58**	**0.63**
Betula pubescens	Total	**Tree density**	**2.45**	**0**
		Wolf utilization	4.73	2.28
		Average tree height	13.3	10.85
	Apical shoot	**Wolf utilization**	**-29.91**	**0**
		Tree density	-26.8	3.11
		Average tree height	-18.66	11.25
	Lateral shoot	**Tree density**	**1.78**	**0**
		Wolf utilization	4.31	2.53
		Average tree height	9.78	8
Picea abies	Total	**Wolf utilization**	**-20.3**	**0**
		Tree density	-16.6	3.7
		Average tree height	-8.6	11.7
	Apical shoot	**Tree density**	**-95.08**	**0**
		Wolf utilization	**-94.8**	**0.28**
		Average tree height	-87.85	7.23
	Lateral shoot	**Wolf utilization**	**-20.78**	**0**
		Tree density	-17.19	3.59

		Average tree height	Error	
Pinus sylvestris	Total	**Tree density**	**35.8**	**0**
		Average tree height	43.4	7.6
		Wolf utilization	Error	
	Apical shoot	**Wolf utilization**	**-13.20**	**0**
		Average tree height	-1.69	11.51
		Tree density	Error	
	Lateral shoot	**Tree density**	**35.5**	**0**
		Wolf utilization	**36.63**	**1.13**
		Average tree height	41.41	5.91
Sorbus aucuparia	Total	**Wolf utilization**	**31.2**	**0**
		Tree density	**32.3**	**1.1**
		Average tree height	39.8	8.6
	Apical shoot	**Tree density**	**52.84**	**0**
		Wolf utilization	**53.14**	**0.3**
		Average tree height	59.83	6.99
	Lateral shoot	**Wolf utilization**	**25.85**	**0**
		Tree density	**25.98**	**0.13**
		Average tree height	28.52	2.67

Species	Browsing data	Fixed factor	Value	P-value
Betula pendula	Total	Wolf utilization	-0.266	0.193
		Tree density	**-0.309**	**0.052**
	Apical shoot	Wolf utilization	-0.139	0.184
		Tree density	**-0.137**	**0.075**
	Lateral shoot	Wolf utilization	0.269	0.193
		Tree density	**-0.338**	**0.031**
		Average tree height	**-0.008**	**0.000**
Betula pubescens	Total	**Tree density**	**-0.173**	**0.028**
	Apical shoot	Wolf utilization	-0.101	0.117
	Lateral shoot	**Tree density**	**-0.168**	**0.032**
Picea abies	Total	Wolf utilization	-0.084	0.158
	Apical shoot	Wolf utilization	0.000	0.967
		Tree density	-0.003	0.692
	Lateral shoot	Wolf utilization	-0.082	0.159
Pinus sylvestris	Total	Tree density	-0.225	0.227
	Apical shoot	Wolf utilization	0.083	0.404
	Lateral shoot	Wolf utilization	0.066	0.810
		Tree density	-0.235	0.206
Sorbus aucuparia	Total	Wolf utilization	-0.213	0.269
		Tree density	-0.159	0.406
	Apical shoot	Wolf utilization	-0.142	0.639
		Tree density	-0.102	0.766
	Lateral shoot	Wolf utilization	-0.107	0.434
		Tree density	0.094	0.564

Annex 2

Browsing variable	Fixed factor	AIC	ΔAIC
Total	**Tree height**	**3621.5**	**0**
	Wolf utilization + Tree height	**3622.8**	**1.3**
	Wolf utilization + Distance + Tree height	3624.5	3.0
	Wolf utiliziation	3636.5	15.0
	Distance	3636.6	15.1
	Tree density	3637.7	16.2
	Wolf utilization + Distance	3638.3	16.8
	Wolf utilization * Distance	3638.7	17.2
Apical shoot	**Tree height**	**2166.3**	**0**
	Wolf utilization + Tree height	**2168**	**1.7**
	Wolf utilization + Distance + Tree height	2168.9	2.6
	Wolf utilziation	2195.3	29.0
	Tree density	2195.7	29.4
	Wolf utilization + Distance	2196.1	29.8
	Distance	2196.9	30.6
	Wolf utilization * Distance	2198.1	31.8
Lateral shoot	**Tree height**	**109.8**	**0**
	Wolf utilization + Tree height	117.2	7.4
	Wolf utilization + Distance + Tree height	133.1	23.3
	Wolf utilziation	137.2	27.4
	Distance	139.1	29.3
	Tree density	146.3	36.5
	Wolf utilization + Distance	152.9	43.1
	Wolf utilization * Distance	168.6	58.8

Species	Browsing data	Fixed factor	Value	P-value
Betula pendula	Total	Wolf utilization + Distance + Tree height	-0.539 -0.008 -0.004	0.128 0.041 0.129
		Wolf utilization + Distance	-0.647 -0.008	0.074 0.042
		Distance	-0.008	0.035
		Wolf utilization + Tree height	-0.533 -0.004	0.110 0.132
	Apical shoot	Tree height	-0.011	0.000
		Wolf utilization + Tree height	-0.153 -0.011	0.572 0.000
	Lateral shoot	Wolf utilization	-0.111	0.129
Betula pubescens	Total	Tree height	-0.005	0.017
		Wolf utilization + Distance + Tree height	-0.399 0.006 -0.005	0.313 0.098 0.034
		Wolf utilization + Tree height	-0.400 -0.005	0.313 0.026
	Apical shoot	Wolf utilization + Tree height	-0.577 -0.011	0.044 0.002
		Wolf utilization + Distance + Tree height	-0.578 0.005 -0.010	0.042 0.228 0.002
		Tree height	-0.012	0.000
	Lateral shoot	Wolf utilization	-0.064	0.150
Picea abies	Total	Wolf utilization + Distance	-1.09 -0.011	0.037 0.096
		Wolf utilization	-1.107	0.023
		Wolf utilization + Distance + Tree height	-1.13 -0.012 0.004	0.033 0.072 0.425

		Wolf utilization * Distance	-1.366 -0.014 Interaction: 0.008	0.057 0.090 Interaction: 0.563
		Distance	-0.012	0.065
	Apical shoot	Tree height	-0.045	0.167
		Wolf utilization + Tree height	0.105 -0.046	0.909 0.168
	Lateral shoot	Wolf utilization	-0.018	0.121
Pinus sylvestris	Total	Tree height	0.012	0.076
		Wolf utilization + Distance + Tree height	-0.667 0.011 0.016	0.087 0.134 0.019
		Wolf utilization + Tree height	-0.689 0.014	0.149 0.045
	Apical shoot	Wolf utilization	1.293	0.234
		Tree density	-0.935	0.339
		Distance	-0.012	0.545
		Tree height	-0.000	0.973
		Wolf utilization + Distance	1.244 -0.008	0.266 0.692
	Lateral shoot	Wolf utilization	0.004	0.932
		Tree density	-0.017	0.541
Sorbus aucuparia	Total	Wolf utilization * Distance	-14.88 -0.200 Interaction: 0.232	0.331 0.312 Interaction: 0.245
	Apical shoot	Distance	0.015	0.090
		Wolf utilization + Distance	-0.081 0.015	0.888 0.092
	Lateral shoot	Wolf utilization	-0.046	0.730
		Tree density	0.036	0.752

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